

ECOLOGY AND MORPHOLOGICAL VARIATION IN
PLACOSTYLUS BOLLONSI (GASTROPODA:
BULIMULIDAE) AT THREE KINGS ISLANDS,
NEW ZEALAND

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Abstract. Five extant and one extinct populations of the local endemic landsnail *Placostylus bollonsi* Suter are known from Three Kings Islands. Morphometric data show that there are consistent differences between the populations in shell characters, and historical information indicates that those morphological differences are probably largely hereditary. The populations on West and North East Islands are estimated to comprise at least 100 and 200 individuals respectively. The extant populations on Great Island were reduced to very low numbers earlier this century after habitat destruction by feral goats, but have increased markedly in size and range since 1946 in response to regeneration of broadleaf vegetation following the removal of goats from the island. In March 1991 it was estimated that the *P. b. bollonsi* population covered an area of about 1.69 ha and numbered at least 210 individuals, the *P. b. caperatus* population covered an area of about 0.49 ha and numbered at least 130 individuals, and the *P. b. arbutus* population covered an area of about 2.7 ha and comprised at least 360 individuals.

Adult *P. bollonsi* snails are believed to lay small numbers of relatively large eggs up to 18 mm long in spring and/or early summer, with most eggs hatching by late summer. Size frequency data indicate the possibility that juvenile snails increase in length by about 25-30 mm/year, and attain adult size at about 3 years old. Rates of turnover of adults in populations are not known, but the average age of adult snails is likely to be at least 8-10 years given the very low proportions of juvenile size classes in populations. Size frequency data for empty shells suggest that at least 60% of snails fail to attain adult size, and indicate that relative mortality rates of hatchlings (i.e. shells <20 mm high) are significantly higher than those of larger juveniles. Mortality of *P. bollonsi* is inferred to occur predominantly as a result of desiccation or old age; there is no evidence that predation is a significant cause of mortality.

The principal factors determining the distribution of *P. bollonsi* snails within colonies appear to be the presence of broadleaf food plants, and sheltered microhabitats in broadleaf litter or under groundcover plants. *P. bollonsi* occurs at densities of up to 2-6 snails/m² in local patches, but overall mean densities of populations determined from 25 m² quadrats range from 0.15-0.35 snails/m².

Three Kings Islands, 60 km NW of Cape Reinga, are a WSW-trending island chain comprising one large island of 407 ha (Great Island), three smaller islands of 10-40 ha each (North East, West and South West Islands), and several islets and rocks up to 5 ha (Figs. 1, 2). Terrestrial habitats at Three Kings Islands support a large number of endemic taxa, including plants (Oliver 1948; Baylis 1951a; Cranwell 1962), earthworms (Lee 1959), molluscs (Powell 1948, 1951; Climo 1973), arthropods (e.g. Salmon 1948a, 1948b, 1948c; Woodward 1950, 1954; Forster 1954; Given 1954; Marples 1956; Giles 1958; Holloway 1963), a skink (McCann 1955), and a subspecies of bellbird (Falla 1948). This report is concerned with one of the Three Kings Islands endemics, the large landsnail *Placostylus bollonsi*. Five geographically isolated extant populations of *P. bollonsi* are present at Three Kings Islands, comprising one on each of West and North East Islands, and three on Great Island. There is also an extinct population of the species known from near Hapuka Point, Great Island.

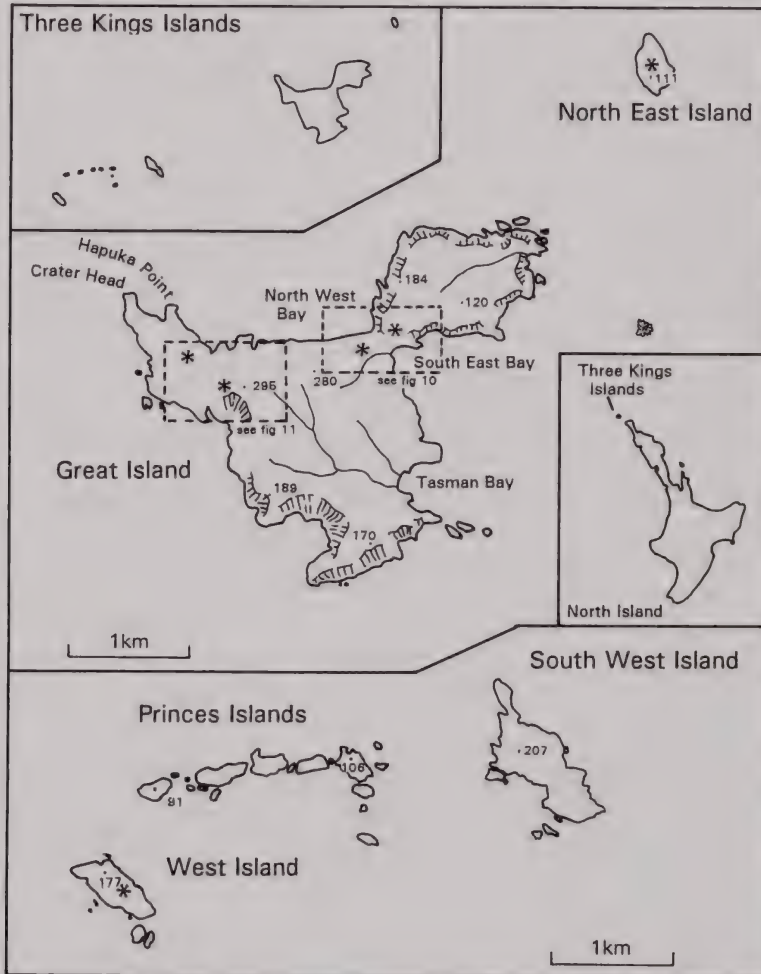


Fig. 1. Geography of Three Kings Islands (Manawa Tawhi), with asterisks denoting locations of *Placostylus bollonsi* Suter populations. Spot heights of islands are given in metres. Areas on Great Island enclosed in boxes are shown enlarged in Figs. 10 and 11.

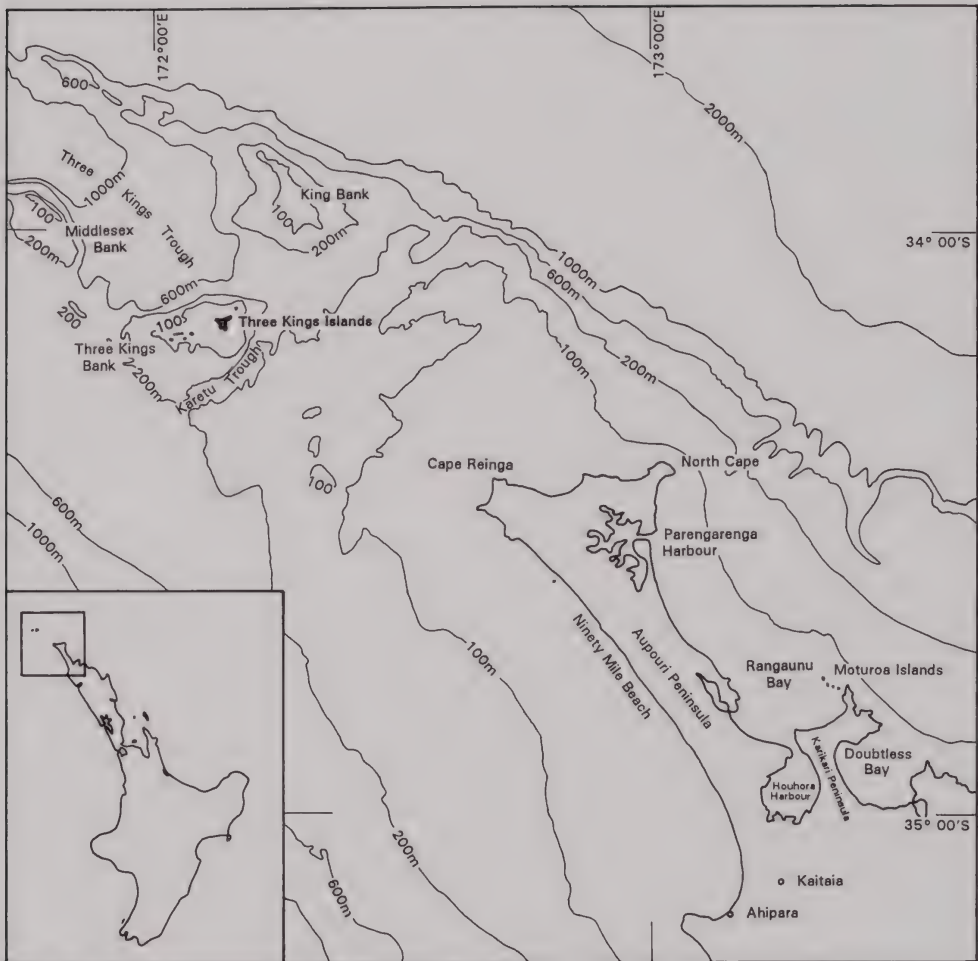


Fig. 2. Location and bathymetric setting of Three Kings Islands, northern New Zealand.

This study was undertaken with three aims directed at assessing the conservation status of populations of *P. bollonsi*. The first aim was to obtain basic information on the population structure and life history of the species. The second was to assess changes in the size and range of *P. bollonsi* populations on Great Island, since censuses carried out in 1945-46 and 1970 by A.W.B. Powell and F.M. Climo respectively (Powell 1948, Climo 1973). The third aim was to obtain morphometric information on shell shapes in populations of *P. bollonsi* collected in 1946-51 and 1982-83, to assess the nature of spatial and temporal morphological variation within and between populations. The purpose of carrying out the morphometric study was firstly, to provide a reassessment of the qualitatively determined morphological groupings of Powell (1948, 1951), and secondly, to assess the relative influences of environmental induction and genetic selection on shell character polymorphism within *P. bollonsi*.

Physical Setting

Islands of the Three Kings group are topographically rugged, having maximum elevations of about 90-295 m, and are mostly bounded by precipitous cliffs. The only beaches are cobble-boulder beaches in North West and South East Bays on Great Island, and that island is the only one large enough to have permanent streams. No meteorological data are available for Three Kings Islands, the nearest recording station being at Cape Reinga on the adjacent mainland coast (Fig. 2). Geographic proximity, and comparable elevation, topography and oceanic influence suggest that the two areas probably have similar climates, although that at Three Kings Islands is likely to be slightly milder and drier. New Zealand Meteorological Service records from Cape Reinga for the period 1919-1980 indicate that mean monthly rainfall was lowest for January (58 mm) and highest for June and July (118-120 mm). For the period 1951-1980, monthly averages of daily maximum and minimum temperatures were highest for February (22.1 °C and 16.4 °C respectively), and lowest for July (14.3 °C and 9.9 °C respectively).

Geological History

Three Kings Islands and at least part of the submarine plateau on which they are located (i.e. Three Kings Bank, Fig. 2) are formed of indurated, highly deformed and altered marine sedimentary and volcanic rocks of probable early Cretaceous age (Hayward & Moore 1987; Brook 1989). The Cretaceous to early Cenozoic history of northern New Zealand is poorly known, but it is possible that marine conditions persisted in the vicinity of present day Three Kings Islands for much or all of that time. The present structural configuration of the northernmost New Zealand area is inferred to have developed largely during the mid Cenozoic. In early Miocene time (c. 15-20 Ma), an antiformal ridge bounded to the NE by a wrench fault zone is believed to have formed a subaerial peninsula extending from the present-day Kaitaia and Doubtless Bay areas, to at least as far NW as the Three Kings Islands area (Brook & Thrasher 1991). This is probably the only period in the mid to late Cenozoic during which a continuous land connection existed between Northland and the Three Kings Islands area. By mid-late Miocene time that ridge is inferred to have foundered, but small land areas probably persisted as islands in the present-day Reinga-North Cape and Three Kings Islands areas. Continued movement along the NW-trending wrench fault zone during this period produced a steep continental slope off northeastern Northland, and led to formation of Three Kings Trough, North Maria Ridge and King Bank, and Karetu Trough (Fig. 2). In late Miocene time (i.e. prior to 8 Ma) much of northern Northland was uplifted by a few hundred metres as indicated by the presence of high level marine-cut terraces (Brook & Thrasher 1991). Erosional terrace remnants at 70-110 m elevation on Three Kings Islands were probably also cut during this period (cf. Hayward & Moore 1987), and point to an increase in land area on Three Kings Bank concomitant with uplift. There is no evidence that major tectonism has occurred on or adjacent to northernmost New Zealand since Pliocene time and topographic features such as Three Kings Bank, Karetu Trough and a broad shelf north and west of Reinga are inferred to have existed in more-or-less their present form since at least that time (Brook & Thrasher 1991).

Cyclical global climate changes and associated glacio-eustatic sealevel fluctuations had major effects on the distribution of land areas in Pliocene and Pleistocene time. Lowered sealevels during glacial periods would have caused significant increases in land areas in northernmost New Zealand and on Three Kings Bank, and islands would have been

present at times on Middlesex and King banks. The depth of Karetu Trough ensured that Three Kings Islands would have remained geographically isolated from mainland Northland during Pliocene-Pleistocene time, but the intervening marine strait would have narrowed to as little as 10 km wide during some Pleistocene glacial periods.

During the peak of the ultimate glaciation from about 18-20 Ka when sealevel was about 120 m lower than at present, all islands in the Three Kings group would have been part of a single landmass of about 120 km² in area. By extrapolating from present-day bathymetry using sealevel curves of Carter *et al.* (1983) and Gibb (1986), it is inferred that the islands would have remained connected during the subsequent post-glacial sealevel rise until about 11-14 Ka. The latest Pleistocene to Holocene geological history of the Three Kings area has thus been one of fragmentation and reduction of terrestrial habitat areas, and associated profound climatic changes, during the transition from glacial to interglacial conditions (cf. Stevens *et al.* 1988).

Anthropogenic Modification

A population of Maori lived permanently on Three Kings Islands for one or more periods in prehistoric time (i.e. pre 1800) as indicated by the presence of numerous cultivation and dwelling sites on Great and North East Islands, and an area of cultivation sites on South West Island (Hayward 1987). Anthropogenic terraces, midden and a burial site are present on West Island, but there is no evidence that that island was ever occupied for long (Baylis 1958; Hayward 1987). Early European records suggest that Three Kings Islands were probably inhabited by Maori for much of the 17th and 18th centuries (Baylis 1948; Hayward 1987). Abel Tasman recorded the presence of cultivated areas and at least 30-35 Maori on Great Island in January 1643, and noted an apparent absence of trees on the island at that time (Heeres 1898). Marion du Fresne found that Great Island was occupied by Maori in 1772 and described it as being grassy with groves of bushes and having a barren appearance (Roth 1891). D'Entrecasteaux recorded Maori occupation of North East Island in 1793 (Labillardière 1799). There was apparently sporadic occupation of Three Kings Islands during the early part of the 19th century, with the last long term Maori occupation occurring on Great Island between the 1830s and about 1840 (Puckey 1836; Cheeseman 1888; McNab 1908; Baylis 1948).

Available information suggests that all of the larger islands in the Three Kings group had a cover of coastal broadleaf forest before human occupation, but that almost all original forest on Great and North East Islands, and probably also much or all of that on South West Island, was cleared by prehistoric Maori in the process of preparing cultivation sites or obtaining fuel (Baylis 1948, 1958; Hayward 1987). Patchwork forest regeneration may have occurred if areas were temporarily retired from cultivation because of nutrient depletion (cf. Leach 1984), but original forest remnants probably only persisted in areas that were too steep or rocky for cultivation. Maori apparently kept pigs and goats on Great Island during the early part of the 19th century (Baylis 1948), and feeding and trampling by those animals would almost certainly have had an effect on the indigenous fauna and flora.

There has been no long term occupation of Three Kings Islands since departure of the last Maori population from Great Island at about 1840, but small groups of people have subsequently visited the islands. Parts of Great Island were fired in the early part of the 20th century (Baylis 1948; Doak 1969), but the greatest modification of that island since the end

of Maori occupation occurred as a result of browsing and trampling by feral goats. There is no direct record as to whether or not any goats were left behind by departing Maori. Botanical surveys carried out on Great Island in 1887 and 1889 (Cheeseman 1888, 1891) record kanuka (*Kunzea ericoides*) and manuka (*Leptospermum scoparium*) as the dominant vegetation cover, but with common admixed broadleaf shrubs and small trees. The presence of abundant plants of highly palatable broadleaf and herb species on the island at that time suggests that goats were probably absent (Baylis 1948, 1986). In 1889 4 goats were liberated on Great Island and a further 2 goats were landed on South West Island to provide a source of food for possible future castaways (Baylis 1948). The goats on South West Island apparently failed to establish (Buddle 1948). However, those on Great Island multiplied rapidly, becoming plentiful by 1903 (D.G. Matthew, pers. comm. in Baylis 1948), and numbering about 300 in 1928 (Fraser 1929). The goat population on Great Island was exterminated in 1946, with a total of 393 individuals being killed (Turbott 1948). Between 1889 and 1946, goats on Great Island had the effect of maintaining a kanuka-dominated subclimax vegetation cover by preventing broadleaf regeneration, and they also caused the extreme reduction and local extinction of several plant species (Baylis 1948, Turbott 1948). Scattered broadleaf trees and a few small remnant broadleaf groves survived locally on steep and/or rocky areas on Great Island, and some shrub and herb species were restricted to sites on coastal cliffs (Baylis 1948). Regeneration of most of the palatable tree, shrub, herb and fern species was rapid and widespread following the removal of goats (Baylis 1948, 1951b; Holdsworth 1951; Holdsworth & Baylis 1967; Cameron *et al.* 1987), but kanuka has persisted as the dominant canopy cover over much of the island.

In contrast to Great Island, broadleaf forest dominated by large pukaniu (*Meryta sinclairii*) and pohutukawa (*Metrosideros excelsa*) trees was established over much of the formerly cultivated top of North East Island by 1947-55, with kanuka being dominant locally in forest and shrubland near the summit, and common in fringing shrubland on the upper slopes of the island (Buddle 1948, Baylis 1958). The vegetation cover of North East Island, including a small patch of bracken thought to be of anthropogenic origin (Baylis 1958), has apparently subsequently changed little from that described in 1947-55.

The vegetation cover on South West Island in the late 19th century consisted of pukaniu-dominated forest on the upper slopes, and shrublands with common manuka and kanuka over much of the rest of the island (Cheeseman 1891). Pukanui-dominated forest subsequently spread to cover just about all except the coastal cliffs, leading to the elimination of manuka and virtual disappearance of kanuka from the island by 1950-52 (Baylis 1958).

Differences in the relative proportions of kanuka/manuka-dominated and broadleaf-dominated forest cover, and observed temporal displacement of kanuka and manuka by pukaniu, led Baylis (1958) to conclude that Great, North East and South West Islands represent a series of stages in the regeneration of indigenous broadleaf communities. This suggests the possibility that Maori occupation may have persisted longer on North East Island than it did on South West Island (Baylis 1958), assuming that rates of vegetation succession on the two islands are similar.

West Island is thought to be the only large island in the Three Kings group on which indigenous broadleaf forest and shrubland communities were not extensively modified or largely destroyed by human activities (Baylis 1958).

Previous Work on *Placostylus bollonsi*

Lesson & Martinet (1884: 227) referred to the existence of a species of *Placostylus* recorded as *Bulimus vibratus* that was reputedly common at Three Kings Islands and that differed from *Placostylus* on mainland Northland. The first known specimens collected were obtained from above the landing in South East Bay, Great Island in April 1907, and described as *Placostylus bollonsi* by Suter (1908). Haas (1935) subsequently placed the species in an endemic monotypic subgenus *Basileostylus*. *P. bollonsi* was considered to have become extinct by 1920, and searches of Great Island in 1928 and 1934 also failed to locate any living snails (Fraser 1929; Powell 1935, 1938, 1948). However, during 1945-46 three small extant colonies were found above South East and North West Bays and south of Crater Head on Great Island, and larger populations were discovered on North East Island in 1947, and on West Island in 1950 (Buddle 1948; Powell 1948, 1951). Snails from the North West Bay and Crater Head colonies were found to have distinctive shell morphologies and were described as *P. bollonsi caperatus* and *P. bollonsi arbutus* respectively by Powell (1948), whereas the snails from South East Bay and North East and West Islands were considered by Powell (1948, 1951) to be comparable with typical *P. bollonsi*. Powell (1948, 1951) attributed the geographic distribution of subspecies of *Placostylus* on Three Kings Islands to the effects of prehistoric human modification of vegetation cover, and to inter-island transferrals by Maori. Climo (1973) discussed the distribution and taxonomic relationships of *P. bollonsi* populations, described the reproductive system of the species, and presented data showing that all three extant colonies on Great Island had undergone increases in population size and range between 1946 and 1970.

METHODS

Population Structure

Size frequency data were obtained for *P. bollonsi* populations on Great Island in March 1991. Four 25 m² quadrats were sampled in the areas occupied by each of the three colonies. The distribution of habitat types containing live *P. bollonsi* snails was determined within each colony area, and quadrats were randomly sited within those. Within each quadrat a thorough search was made for all living and dead *P. bollonsi*. Shell lengths of those found were measured on site, and specimens were then returned to the quadrat area; live snails were replaced within broadleaf litter, whereas dead shells were scattered randomly throughout the quadrat.

A distinction was made between living and dead specimens, and between specimens possessing a labial varix and those with an unthickened outer lip. Callus deposition around the apertural margin of *P. bollonsi* shells does not begin until an individual has almost attained maximum shell length, and thus the presence of a varix is a useful criterion for distinguishing 'adult' from 'juvenile' shell morphological types.

Qualitative observations on *P. bollonsi* colonies on North East and West Islands were made during brief visits in 1982-83.

Population Size and Range

The geographic extent of each of the *P. bollonsi* colonies on Great Island was determined in November 1983 and March 1991, by searching for live snails and shells of recently dead snails, and recording their distribution on a 1:10 000 scale topographical map (i.e. enlargement of Department of Survey and Land Information NZMS 270 Sheet L01). Brief field notes were made on the distribution of gross vegetation types within and adjacent to each colony, and abundances of live snails in habitats were qualitatively assessed. Estimates of population sizes of the three colonies in 1983 and 1991 are made on the basis of geographic areas occupied by snails, known and inferred densities of live snails as determined from quadrats and qualitative observations, and assessment of the proportion of habitat containing snails within each colony.

Morphometric Analysis

Randomly selected samples of 20 empty adult *Placostylus* shells retaining periostracum and apertural colour, and with no obvious growth abnormalities, were made at sites within each of the colonies on North East, West and Great Islands during 1982-83. Shells collected from the same colonies in 1946-51, numbering 8-12 individuals per site, were examined in collections held at the Auckland Institute and Museum, and the National Museum of New Zealand, Wellington. The holotype of *P. bollonsi* Suter collected in 1907, and 9 shells collected in 1946 from an extinct colony near Hapuka Point on Great Island were also included in biometric analyses. Locality data for the samples are given in Appendix 1.

Ten linear measurements of shell dimensions of each of 160 shells were made to the nearest 0.1 mm using vernier callipers (Fig. 3). These characters were selected to determine differences in shell height, apertural height, spire angle and whorl inflation within and between populations. All measurements were made by one person (FJB).

Principal components analysis was carried out on a correlation matrix of the total multivariate data set using the PRINCOMP procedure in the SAS statistical package (SAS/STAT users guide, 6.03 ed.; SAS Institute, Cary, North Carolina 1988). The significance of temporal variation in shell height and apertural height between 1946-51 and 1982-83 samples from each of the five extant *P. bollonsi* populations was assessed using two-tailed t-tests.

RESULTS

Population Structure

This section presents information on size frequency, density and mortality within *P. bollonsi* populations on Great Island as obtained from quadrat studies and general observations, and gives brief descriptions of populations on West and North East Islands.

Great Island Colonies

Size frequency data for live *P. bollonsi* on Great Island, as determined from searches of four 25 m² quadrats within each colony in March 1991, are shown in Figs. 4-6. Adult

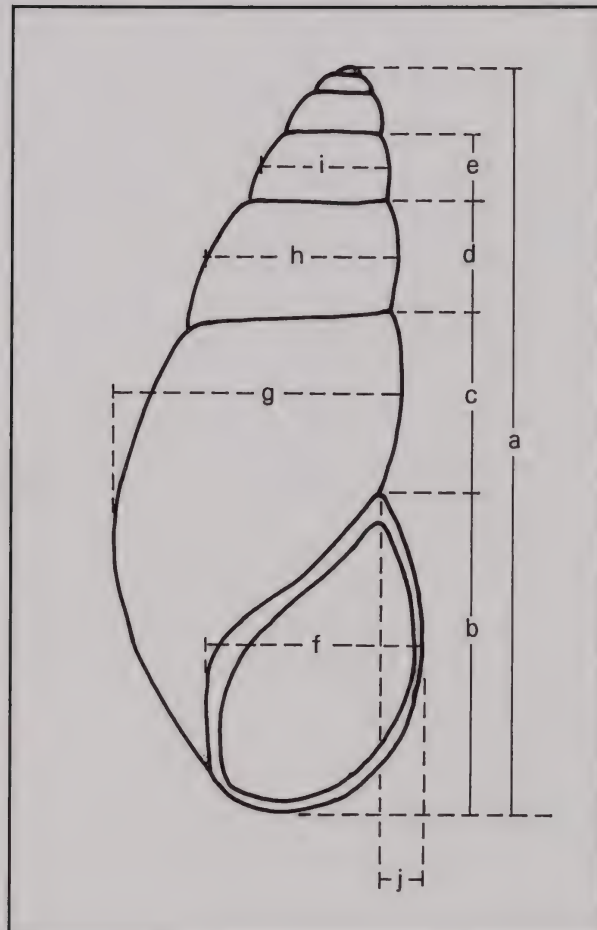
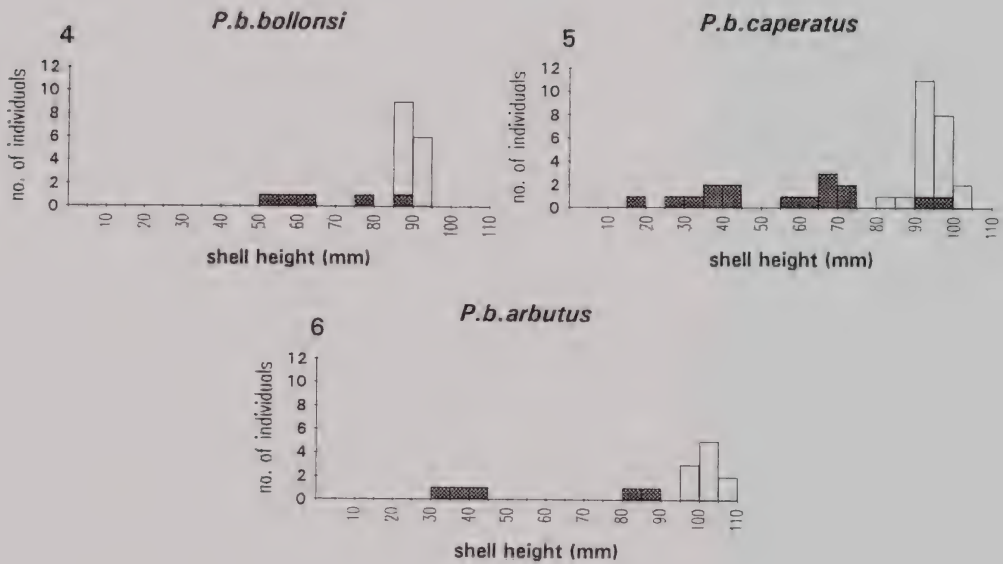


Fig. 3. Dimensions of *P. bollonsi* shells used for morphometric analysis.

snails predominate within areas surveyed in the *P. b. bollonsi* and *P. b. arbutus* colonies (74% and 67% of populations respectively), but were found to occur in subequal proportions to juveniles within the *P. b. caperatus* colony (i.e. 57% adults). Only one of the individual 25 m² quadrats contained more juvenile than adult snails, but qualitative observations made within all three colonies indicate that juveniles predominate locally in peripheral areas.

Size frequency distribution data for *P. bollonsi* indicate that all populations on Great Island are strongly normally skewed towards adult size classes. Data for *P. b. bollonsi* and *P. b. arbutus* have a single large unimodal peak within the adult size range, whereas those for *P. b. caperatus* show the same large unimodal peak of adult abundance, but also show two smaller peaks of juvenile abundance at shell heights of 35-45 mm and 65-75 mm respectively (Fig. 5). These juvenile peaks perhaps represent annual cohorts of *P. b. caperatus*. If that interpretation is correct it indicates that juvenile shells increase in height by c. 25-30 mm/year (i.e. from a hatchling height of about 11-16 mm), and attain adult size at about 3 years old.



Figs. 4-6. Size frequency distributions of shells of live *P. bollonsi* snails on Great Island in March 1991, based on searches of four 25 m² quadrats within each of the populations. Shaded and unshaded bars denote numbers of individuals with unthickened and thickened outer lips respectively. 4. *P. b. bollonsi*. 5. *P. b. caperatus*. 6. *P. b. arbutus*.

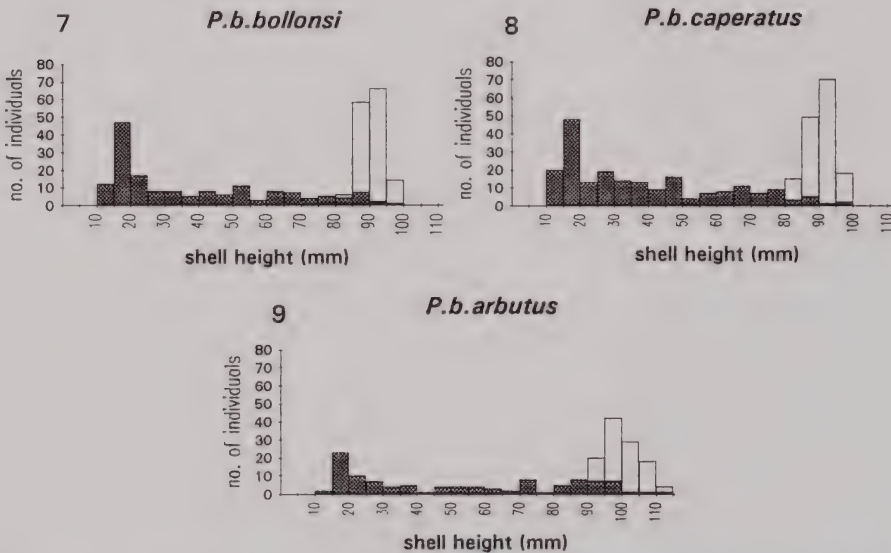
Densities of live *Placostylus* snails recorded in quadrats on Great Island are listed in Table 1. Snails are present at similar densities in the *P. b. bollonsi* and *P. b. arbutus* colonies, but the *P. b. caperatus* colony differs in having considerably higher juvenile densities, and hence higher overall snail densities than the other two colonies. Live snails were typically sparsely and apparently randomly distributed within quadrats that had a gently to moderately sloping substrate and an extensive cover of deep broadleaf litter. However, on steeper slopes and in areas where the leaf litter cover was thinner or less extensive, live snails were generally only present within pockets of broadleaf litter that were stabilised within scree, or by groundcover plants such as *Asplenium oblongifolium* or *Carex testacea*, and behind logs, and the roots and trunks of trees. In such areas the patchy distribution of snails produces marked small scale variation in snail density. Localised densities of up to 2-3 snails/m² were observed within small isolated leaf litter pockets in some quadrats during the 1991 survey, but densities of up to 4-6 snails/m² were recorded locally in comparable microhabitats within the *P. b. caperatus* and *P. b. arbutus* colonies in 1982.

Searches of quadrats on Great Island in March 1991 failed to locate any live *Placostylus* eggs, but rare empty eggs (i.e. lacking a cuticle and with a corroded surface) and a few eggshell fragments were found. In contrast, single eggs were relatively common throughout broadleaf litter within areas occupied by colonies on West and Great Islands in December 1982, and on North East and Great Islands in November 1983, and Climo (1973) noted that numerous eggs were present at each of the three Great Island colonies in November 1970.

Table 1. Mean and range of densities of live *P. bollonsi* on Great Island as determined from four 25 m² quadrats within each colony in March 1991.

		<i>P. b. bollonsi</i>	<i>P. b. caperatus</i>	<i>P. b. arbutus</i>
Adult + juveniles/m ²	mean ± S.E.	0.18 ± 0.03	0.34 ± 0.14	0.15 ± 0.05
	range	0.12 - 0.28	0.08 - 0.72	0.08 - 0.28
Juveniles/m ²	mean ± S.E.	0.05 ± 0.03	0.15 ± 0.07	0.05 ± 0.02
	range	0 - 0.12	0 - 0.32	0 - 0.08
Adults/m ²	mean ± S.E.	0.13 ± 0.04	0.19 ± 0.07	0.1 ± 0.03
	range	0.04 - 0.24	0.08 - 0.4	0.04 - 0.2

Size frequency data for spatially and temporally averaged populations of empty *P. bollonsi* shells, as determined from searches of four 25 m² quadrats within each of the colonies on Great Island, are given in Figs. 7-9. The three shell collections each show similar bimodal distributions, with peaks in adult size classes and in the 15-20 mm juvenile size class. Proportions of juvenile to adult shells are also similar within the three populations comprising 56%, 58% and 53% of the *P. b. bollonsi*, *P. b. caperatus* and *P. b. arbutus* populations respectively. Hatchling shells (10-20 mm size class) are almost certainly under-represented in the collections as a consequence of their being weakly calcified and very fragile compared with larger shells, and thus actual juvenile mortality levels within the colonies on Great Island are probably considerably higher than the assessed percentages.



Figs. 7-9. Size frequency distributions of empty *P. bollonsi* shells based on searches of four 25 m² quadrats within each of the *P. bollonsi* populations on Great Island in March 1991. Shaded and unshaded bars denote numbers of individuals with unthickened and thickened outer lips respectively. 7. *P. b. bollonsi*. 8. *P. b. caperatus*. 9. *P. b. arbutus*.

No examples of *P. bollonsi* shells damaged by predators were seen in quadrats, or elsewhere on Great Island.

West Island

In December 1982, live *P. bollonsi* were found at c. 100 m elevation on the ridge crest at the southeastern end of West Island, and above c. 80 m elevation on the steep SW-facing slope above the Elingamite wreck site. Elsewhere only scattered dead shells were seen. There were at least 50 live individuals present at the southeastern end of the island, in a terraced area under a 3 m high canopy of pukanui, karaka (*Corynocarpus laevigatus*) and Three Kings rangiora (*Brachyglottis arborescens*). Live snails were found only under *Carex* sedges in areas with deep, moist broadleaf litter, but empty shells were present both under *Carex* and throughout adjacent areas of broadleaf litter. Some shells of freshly dead adult snails were present in thin, dry litter at the margin of the grove. Living and dead *P. bollonsi* juveniles were very rare at this locality, but solitary eggs were common in broadleaf litter. No quantitative abundance data were obtained, but clumped densities of up to 3-5 live snails per m² were observed locally. No information is available on the abundance and density of snails on the steep southwestern side of West Island. In that area rare live snails were present in ponded accumulations of broadleaf litter beneath a low mixed broadleaf canopy. The overall population size of *P. bollonsi* on West Island is not known, but it probably comprised at least 100 individuals in 1982.

North East Island

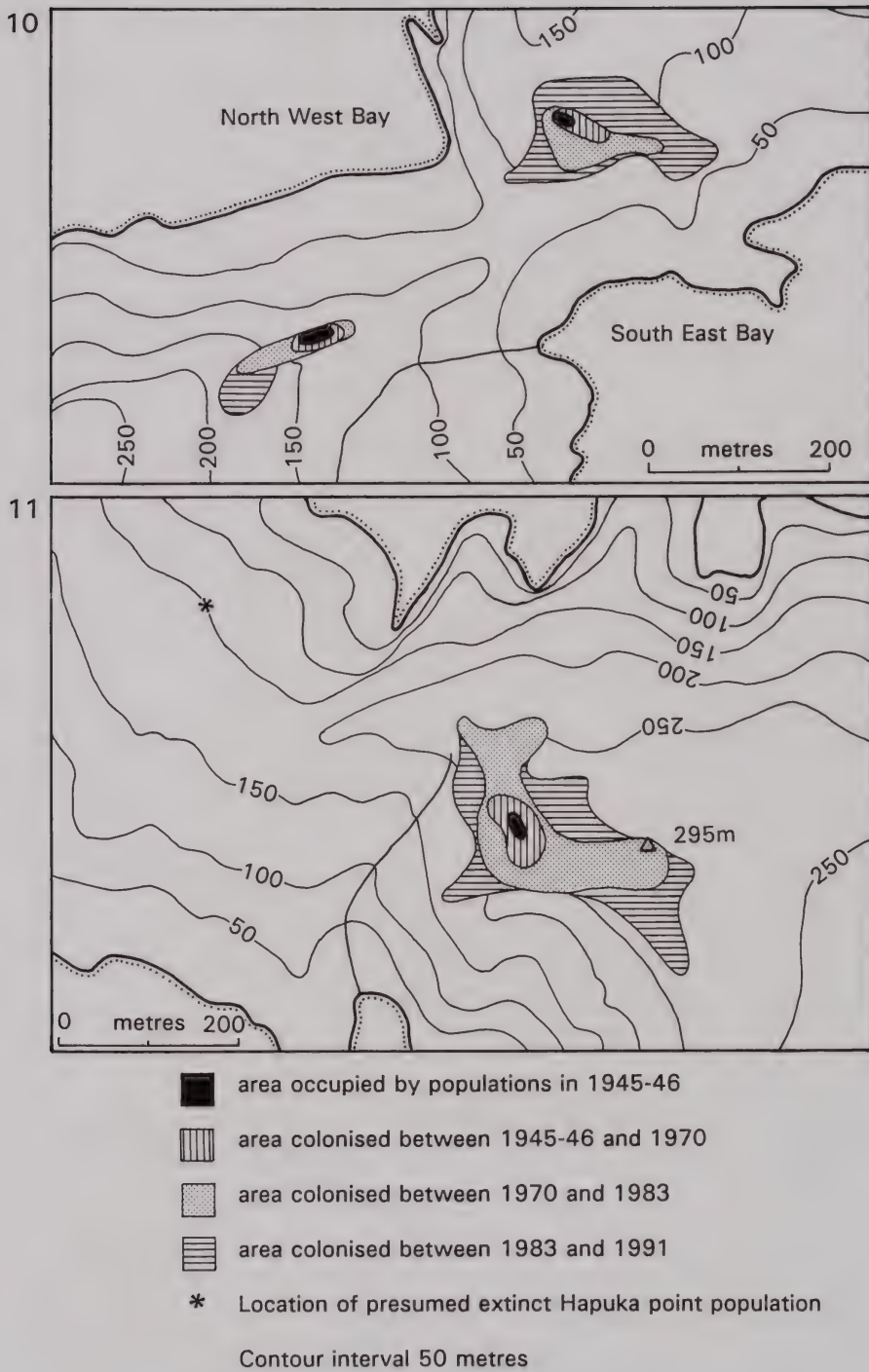
During a brief visit in November 1983, live *P. bollonsi* were found over an area of about 1.5 ha across much of the forested top and upper slopes of North East Island. Snails were scattered throughout litter and under *Carex* and groundferns, beneath a canopy dominated by pukanui with some pohutukawa. Qualitative observations suggest that live adult and juvenile snails were present in similar proportions and densities to *P. b. bollonsi* and *P. b. arbutus* in broadleaf forest on Great Island (see above), indicating that the population on North East Island probably comprised at least 200 individuals in 1983.

Colony Expansion on Great Island, 1945 to 1991

Comparison of 1991 data with those in Powell (1948) and Climo (1973) indicates that all three extant *P. bollonsi* colonies on Great Island have increased substantially in size and range since 1945 (Figs. 10-13). Temporal changes in size and extent of the *P. b. bollonsi*, *P. b. caperatus* and *P. b. arbutus* colonies are described separately below.

P. bollonsi bollonsi Colony

Powell (1948: 283) states that in 1945 this colony covered an area of c. 20 m² on a bouldery slope of about 45°, on the lower side of a long rocky cliff face in moderately dense scrub (see Fig. 10 for location). At that time a total of 11 live adult snails (and no live juveniles) were recorded under the leaf spread area of 7 trees of wharangi (*Melicope ternata*) and 1 of mahoe (*Melicytus ramiflorus*). By 1970 the colony comprised a population of at least 30 live individuals (including juveniles) concentrated near a group of broadleaf trees on the seaward side of the rock escarpment, but also extending sparsely in either



Figs. 10-11. Geographic ranges of *P. bollonsi* populations on Great Island in 1945-46, 1970, 1983 and 1991. The locations of these areas are shown in Fig. 1. 10. *P.b. bollonsi* (upper right) and *P.b. caperatus* (lower left). 11. *P.b. arbutus*.

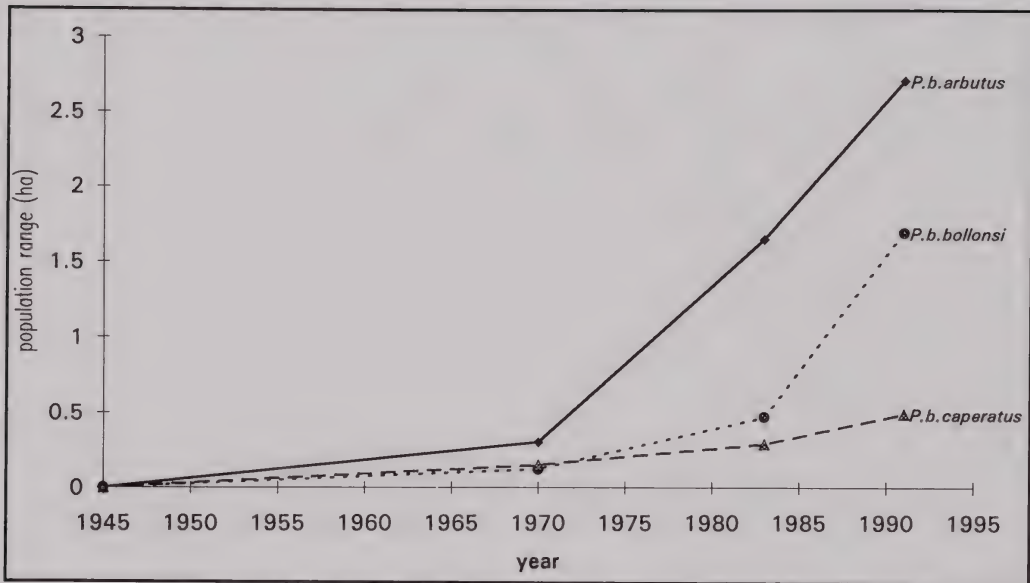


Fig. 12. Estimated range increases of *P. bollonsi* populations on Great Island from 1945-46 to 1991.

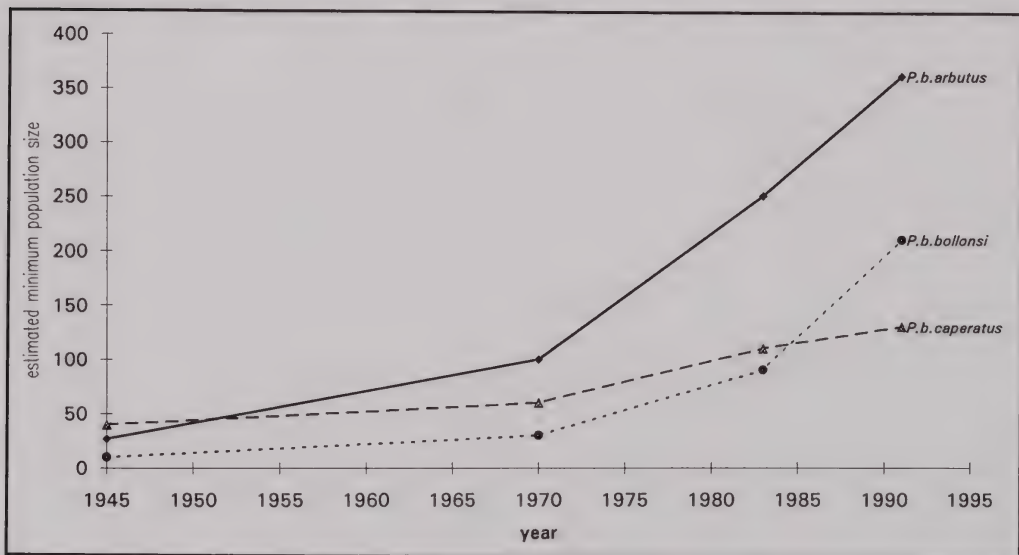


Fig. 13. Estimated minimum sizes of *P. bollonsi* populations on Great Island between 1945-46 and 1991. Data for 1945-46 and 1970 are from Powell (1948) and Climo (1973) respectively. Methods for estimating 1983 and 1991 population sizes are outlined in the text.

direction along the base of the escarpment for a total distance of about 60 m (Climo 1973: 585). Live snails apparently occurred over an area of about 0.12 ha at that time. In 1983 the colony was found to occupy an area of about 0.47 ha, with live snails occurring in mixed broadleaf-kanuka forest for as much as 60 m downslope from the base of the escarpment, and westwards to the ridge at the western end of the escarpment. The colony had also extended to the top of the escarpment into kanuka dominated forest in the east (Fig. 10). By 1991 *P. b. bollonsi* had sparsely colonised an extensive area of kanuka-dominated and broadleaf forest in the valley to the north and east of the escarpment, and rare live snails were also present in pukuanui forest in a steep gully above the head of North West Bay. The area occupied by the colony in March 1991 is estimated to be about 1.7 ha in extent (Figs. 10 and 12). Conservative qualitative assessments indicate that live snails occurred in about 20% of the total colony area occupied by 1983, but that only about 10% of the area colonised between 1983 and 1991 is occupied owing to the patchiness of suitable microhabitats with stable broadleaf litter or other ground cover. Thus live snails are inferred to have been present over total areas of c. 0.1 ha in 1983 and c. 0.25 ha in 1991. If the assumption is made that live snails were present within areas of suitable habitat at an average density of 0.1 snails/m² (i.e. conservative extrapolation from quadrat data - above), then it follows that the estimated minimum size of the *P. b. bollonsi* population would have increased from c. 90 snails in 1983 to 210 snails in 1991 (Fig. 13). The maximum linear extension of the colony periphery for the period 1970-1991 (excluding areas where snails may have rolled or been washed downslope), was approximately 120 m, giving an average rate of increase of about 5-6 m/year.

P. bollonsi caperatus Colony

In 1946 this colony comprised at least 40 living snails in an area of dense ngaio (*Myoporum laetum*) scrub (Powell 1948: 283). Climo (1973: 586) described the colony as being present in a valley on the seaward side of a low rocky escarpment and observed about 60 living snails. He noted that the snails were concentrated on the outer edge of the valley near its higher end in shrubby broadleaf vegetation, but also extended sparsely into kanuka forest adjacent to the escarpment, and down the valley slope. From the description given in Climo (1973) it is estimated that the colony occupied an area of about 0.15 ha in 1970, but by 1983 it had expanded to cover an area of about 0.3 ha (Figs. 10 and 12). Living snails were still concentrated under broadleaf trees and shrubs on the seaward side of the valley in 1983, but also extended 60 m SSW up a boulder escarpment and into mixed broadleaf-kanuka forest and scrub at the head of the valley, and rare snails were present locally under *Carex* sedges in kanuka-broadleaf scrub at the top of the rock escarpment bordering the southeastern side of the valley. The colony subsequently expanded south from the head of the valley into an area of kanuka-dominated forest with common broadleaf shrubs, and by 1991 covered a total area of c. 0.5 ha (Figs. 10 and 12). Conservative qualitative estimates and extrapolations from quantitative quadrat studies (above), suggest that in 1983 and 1991 live snails were present over about 0.06 ha or 20% of the total colony area occupied within the valley at an average density of about 0.2 snails/m². In 1991 living snails are also estimated to have been present over about 0.02 ha or 10% of the colony area to the south of the valley at an average density of about 0.1 snails/m². These estimates, if correct, indicate that the minimum size of the *P. b. caperatus* population would have increased from c. 110 snails in 1983 to 130 snails in 1991 (Fig. 13). Maximum linear extension of the colony periphery for the period 1970-1991 was approximately 110 m, giving an average increase of about 5 m/year.

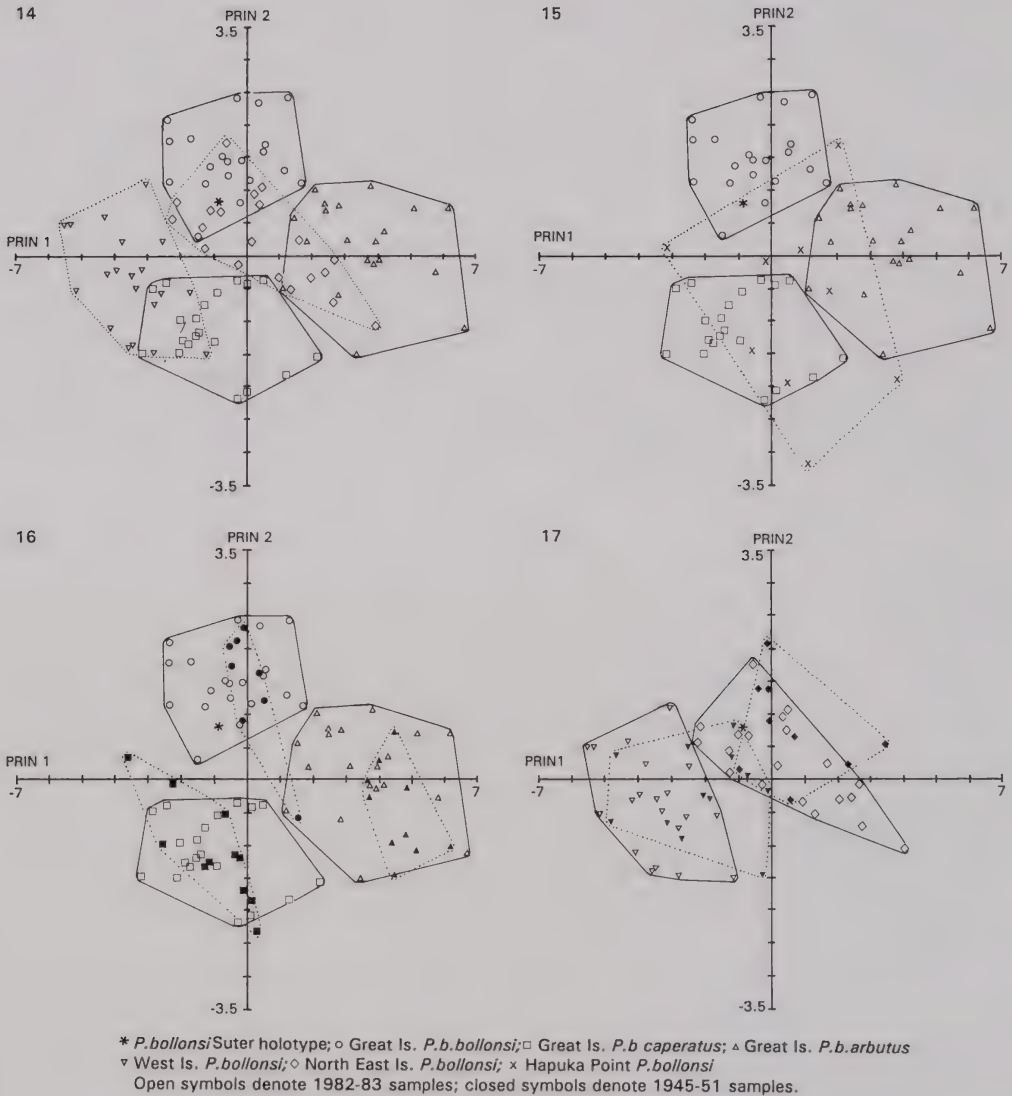
P. bollonsi arbutus Colony

In 1945 this colony was restricted to an area of boulders at the foot of a W-facing scree slope, beneath a small remnant grove of broadleaf trees (Powell 1948: 284). Twenty-five living adult snails (no live juveniles) were observed in broadleaf litter ponded between boulders, but Powell (1948) considered that more than twice that number of snails could have been present. By 1970 the colony included at least 100 living specimens, and had extended up the scree slope to a small cliff marking the upper limit of the valley, south into kanuka forest on the edge of the broadleaf grove at the centre of the colony, and NW down the slope from the rock scree into an area with scattered *Cordyline kaspar* trees (Climo 1973: 585). At that time living snails apparently occurred over an area of about 0.3 ha (Figs. 11 and 12). The colony increased dramatically in size after 1970, expanding into kanuka-broadleaf forest and shrubland on ridge crests to the north and east, and extending further downslope to the west within mixed kanuka- broadleaf-*Cordyline* forest (Fig. 11). The *P. b. arbutus* colony is estimated to have had a range of about 1.65 ha in 1983 and 2.7 ha in 1991 (Fig. 12). On the basis of qualitative observations, and extrapolation from quadrat data (above), it is estimated that in 1983 and 1991 snails were present in about 20% of the colony area centred on the remnant broadleaf grove (i.e. the 0.3 ha occupied by 1970), at an average density of c. 0.2 snails/m². Coverage and densities of snails elsewhere within the colony in 1983 and 1991 were lower as a consequence of the patchiness of broadleaf vegetation and areas of stable broadleaf litter. Live snails were conservatively estimated to have been present in about 10% of the area colonised between 1970 and 1991, at an average density of c. 0.1 snails/m². On the basis of those estimates the minimum size of the *P. b. arbutus* population would have increased from c. 250 individuals in 1983 to 360 individuals in 1991 (Fig. 13). Maximum linear extension of the colony periphery for the period 1970- 1991 was approximately 240 m, giving an average rate of increase of about 11 m/year.

Morphometric Analysis

The results of principal components analysis (PCA) on a multivariate data set incorporating the *P. bollonsi* Suter holotype, and samples of shells collected from *P. bollonsi* colonies on North East, Great and West Islands in 1945-51 and 1982-83 are given in Figs. 14-17. Cumulative eigenvalues of the correlation matrices for Prin 1 + Prin 2 describe 81% of variability within the data set. Significant features of this PCA plot with respect to variation within the 1982-83 samples (i.e. Figs. 14-17) are:

- (1) The 3 samples from extant Great Island populations form discrete, non-overlapping albeit adjacent fields.
- (2) The field defined by the North East Island sample is partly overlapping with those of the *P. b. bollonsi* and *P. b. arbutus* samples (cf. Powell 1948).
- (3) The field defined by the West Island sample is partly overlapping with that of the *P. b. caperatus* sample, but does not overlap with the *P. b. bollonsi* field (cf. Powell 1951).
- (4) The *P. bollonsi* Suter holotype plots within fields defined by both the *P. b. bollonsi* and North East Island samples.
- (5) The field defined by 9 individuals from an extinct *P. bollonsi* colony at Hapuka Point on Great Island is partly overlapping with fields defined by samples from each of the 3 extant populations on Great Island.



Figs. 14-17. Two dimensional configuration produced by principal components analysis of a multivariate morphometric data set incorporating shell measurements from the *P. bollonsi* Suter holotype, and from samples collected from *P. bollonsi* populations in 1945-51 and 1982-83. 14. Samples collected from the five extant populations in 1982-83. 15. Samples collected from the 3 extant Great Island populations in 1982 and from an extinct population at Hapuka Point in 1946. 16. Pairs of samples collected from extant Great Island populations in 1945-46 and 1982. 17. Pairs of samples collected from populations on West and North East Islands in 1947-51 and 1982-83.

A comparison of 1945-51 and 1982-83 PCA groupings for samples from each of the 5 extant populations (Figs. 16, 17) indicates that ranges of morphological variability shown by the 1982-83 West Island, North East Island and *P. b. caperatus* samples are partly overlapping with those of the respective 1945-51 samples. Data points for 7 out of 8 *P. b. bollonsi* individuals from the 1945 sample are tightly clustered and enclosed within the 1982 *P. b. bollonsi* field, but the 8th data point is markedly disjunct from other *P. b. bollonsi*. The 1945 *P. b. arbutus* field is completely enclosed within the 1982 field in terms of Prin 1 and Prin 2 values (Fig. 16), but shows only partial overlap with respect to ranges of Prin 3 values.

Summarised data and results of t-tests presented in Tables 2 and 3 indicate that there are no significant differences in variance at $\alpha = 0.05$ (two-tailed test) between either shell height or apertural height values within samples collected in 1945-48 and 1982-83 from each of the *P. b. bollonsi*, *P. b. caperatus*, *P. b. arbutus* and North East Island populations. Differences in variance of shell height between 1950-51 and 1982 samples from the West Island population are similarly not significant, whereas differences in variance of apertural height between the two West Island samples are statistically significant at $t_{0.025,30} = \pm 2.042$ and $t = 2.564$.

DISCUSSION

Life History

Placostylus bollonsi snails are hermaphroditic (Climo 1973). Casual observations of temporal variability in abundance of eggs suggest the possibility that egg laying by *P. bollonsi* is seasonal, occurring in spring and/or early summer, with most eggs hatching by late summer. Timing of breeding, and duration of the period between laying and hatching are not known. The large size of *P. bollonsi* eggs (12.5-18.0 mm long) and the fact that they are apparently laid singly, indicate that egg production and laying behaviour of *P. bollonsi* differ from those of *Placostylus* (*Maoristylus*) species. Snails in the latter group lay one dozen to several dozen small eggs (5.7-6.6 mm long) in depressions or 'nests' covered by 10-15 mm of loose soil and leaf litter (Choat and Schiel 1980, Penniket 1981).

There is no direct information on growth rates of *P. bollonsi* but size frequency data for *P. b. caperatus* show 3 evenly spaced size cohorts (4 including hatchlings), suggesting the possibility that snails increase in length by about 25-30 mm/year and attain 'adult' size at about 3 years old. In contrast, *Maoristylus* species are thought to reach adult size in 4-6 years, albeit with growth rates showing positive correlation with the moisture content of leaf litter (Penniket 1981). The rates of turnover of adult snails in *P. bollonsi* populations are not known. However, given that numbers of snails in Great Island populations are increasing rapidly despite the fact that those populations apparently contain only very low proportions of juvenile size classes, it follows that the average age of adult snails is likely to be at least as much as 8-10 years and could be significantly more.

Size frequency data for samples of empty *P. bollonsi* shells suggest that at least 60% of snails fail to attain adult size and indicate that relative mortality rates of hatchlings are significantly higher than those of larger juvenile size classes. Comparison of the size

Table 2. Range, mean and standard deviation of shell height within *P. bollonsi* samples collected from Three Kings Islands in 1945-51 and 1982-83, and results of two-tailed t-tests at $\infty = 0.05$ between means of temporally disjunct samples from each of the extant populations.

Year of collection	Range of shell heights (mm)	Mean shell height \pm S.D. (mm)	Number of individuals	t value at $\infty = 0.05$, and n degrees of freedom.	$t_p =$ difference of pop. means
<i>P. b. bollonsi</i> (Great Island) 1945(-1951?) 1982	88.7-95.4 85.3-98.8	91.5 \pm 2.1 92.1 \pm 3.9	8	$t_{0.025,26} = \pm 2.056$ $t_p = 0.409$	
<i>P. b. caperatus</i> (Great Island) 1946 1982	84.0-97.0 87.1-102.2	91.9 \pm 4.0 93.1 \pm 3.5	11	$t_{0.025,29} = \pm 2.045$ $t_p = 0.87$	
<i>P. b. arbutus</i> (Great Island) 1945 1982	103.4-113.9 99.7-115.0	107.4 \pm 3.1 105.1 \pm 4.1	10	$t_{0.025,28} = \pm 2.048$ $t_p = 1.559$	
<i>P. b. bollonsi sensu lato</i> (Hapuka Pt, Great I.) (extinct) 1946	84.7-102.7	96.0 \pm 5.2	9		
<i>P. b. bollonsi sensu lato</i> (West Island) 1950-51 1982	77.5-90.8 74.8-87.8	84.9 \pm 4.0 82.2 \pm 3.4	12	$t_{0.025,30} = \pm 2.042$ $t_p = 2.036$	
<i>P. b. bollonsi sensu lato</i> (North East Island) 1947-48 1983	91.2-99.2 84.4-100.9	93.6 \pm 2.8 92.5 \pm 5.1	9	$t_{0.025,27} = \pm 2.052$ $t_p = 0.604$	

Table 3. Range, mean and standard deviation of apertural height within *P. bollonsi* samples collected from Three Kings Islands in 1945-51 and 1982-83, and results of two-tailed t-tests at $\infty = 0.05$ between means of temporally disjunct samples from each of the extant populations.

Year of collection	Range of apertural heights (mm)	Mean apertural height \pm S.D. (mm)	Number of individuals per sample	t value at $\infty = 0.05$, and n degrees of freedom.	$t_p =$ difference of pop. means
<i>P. b. bollonsi</i> (Great Island) 1945(-1951?) 1982	38.4-40.1	39.2 \pm 0.6	8	$t_{0.025,26} = \pm 2.056$ $t_p = 0.681$	
<i>P. b. caperatus</i> (Great Island) 1946 1982	33.5-36.6	35.5 \pm 0.9	11	$t_{0.025,29} = \pm 2.045$ $t_p = 1.357$	
<i>P. b. arbutus</i> (Great Island) 1945 1982	41.9-45.2	42.8 \pm 1.0	10	$t_{0.025,28} = \pm 2.048$ $t_p = 1.905$	
<i>P. b. bollonsi sensu lato</i> (Hapuka Pt, Great I.) (extinct) 1946	33.9-41.6	37.7 \pm 2.5	9		
<i>P. b. bollonsi sensu lato</i> (West Island) 1950-51 1982	31.5-38.3	35.1 \pm 1.9	12	$t_{0.025,30} = \pm 2.042$ $t_p = 2.564$	
<i>P. b. bollonsi sensu lato</i> (North East Island) 1947-48 1983	35.6-42.5	39.1 \pm 2.0	9	$t_{0.025,27} = \pm 2.052$ $t_p = 0.156$	

frequency distributions of dead *P. bollonsi* with those of *P. (M.) hongii* populations from areas without introduced mammalian predators (see data for Poor Knights Islands in Choat & Schiel 1980, Penniket 1981), indicates that 'natural' levels of hatchling mortality are markedly higher in the latter species. There appear to be fundamental differences in recruitment strategies between the two New Zealand subgenera of *Placostylus*, with *Maoristylus* producing numerous small eggs and suffering proportionately higher hatchling mortality, whereas *Basileostylus* produces fewer and larger eggs, and has a proportionately greater survival rate of resultant hatchlings.

There is no evidence that predation is a significant cause of mortality in *P. bollonsi*, in spite of the presence of a number of potential predators of small juvenile snails at Three Kings Islands (i.e. birds, reptiles, arthropods). Most juvenile mortality probably occurs as a consequence of desiccation of snails during dry periods, whereas adults probably die mainly of desiccation or old age.

Ecology

P. bollonsi snails occur in forest and shrubland habitats, and are ground-dwelling herbivores. There is no record of the species occurring arboreally. From qualitative observations it appears likely that the principal factors determining the distribution of snails within colonies are the presence of broadleaf food plants, and of sheltered microhabitats under broadleaf litter or groundcover plants (e.g. ferns, *Carex* spp., *Muehlenbeckia complexa*). The preferred food plants of *P. bollonsi* have not been determined, but fallen leaves of various broadleaf shrub and tree species, including pukaniui, karaka, wharangi, mahoe, Three Kings rangiora, ngaio, hangehange (*Geniostoma rupestre* var. *ligustrifolium*), parapara (*Pisonia brunoniana*) and *Coprosma macrocarpa* are probably eaten. Live adult and juvenile snails are typically sparsely and apparently randomly distributed in areas with extensive, stable broadleaf litter, but are clustered in pockets of broadleaf litter or under groundcover vegetation on steep slopes and in areas where broadleaf food plants are sparsely or patchily distributed. *P. bollonsi* occurs at localised densities of up to 2-6 snails/m² within such microhabitat patches, whereas mean densities determined from 25 m² quadrats are much lower, ranging from 0.15-0.35 snails/m². In contrast, *P. (M.) hongii* at Poor Knights Islands is reported as occurring at overall mean densities of 2.11 snails/m² and 8.12 snails/m² on Tawhiti Rahi and Aorangi Islands respectively (Penniket 1981).

P. bollonsi snails under natural conditions are apparently active only at night, remaining sheltered in cryptic microhabitats during daylight. Observations by Climo (1973) suggest that dispersal of snails is random, and that individuals can cover distances of up to several metres per night. Intensity of activity is apparently related to weather conditions, being greater during or following periods of rain. Juvenile snails locally predominate in peripheral areas of colonies on Great Island, suggesting that they are probably at least as active as adults, and play an important role in extending the boundaries of colonies through emigration. Expansion of geographic ranges of the Great Island colonies, and to a lesser extent parallel increases in their population sizes (Figs. 10-13), are evidently in part limited by the nature of the vegetation cover in surrounding habitats. Extensive broadleaf regeneration since 1946 in and adjacent to areas occupied by the *P. b. bollonsi* and *P. b. arbutus* colonies (e.g. Cameron *et al.* 1987), has presumably made it possible for those populations to undergo rapid range expansion, whereas the spread of *P. b. caperatus* has probably been limited by a persistence of kanuka-dominated vegetation

in the surrounding area. Changes in areas occupied by colonies on Great Island since 1970 indicate that *P. bollonsi* snails are capable of crawling up rock escarpments and steep, bare, friable soil slopes, and of moving into small isolated patches of broadleaf vegetation within areas of kanuka forest or shrubland. However, their successful dispersal across areas of inhospitable habitat is probably limited to wet periods when snails would be able to escape desiccation. Given the rapid range expansion of colonies, and the ability of *P. bollonsi* snails to disperse across areas lacking broadleaf vegetation cover or stable litter, Climo's (1973) assertion that the three extant subspecies on Great Island are unlikely to intermingle, is probably incorrect.

Variation in Shell Morphology

Results of the morphometric analysis presented above are subject to the following known and inferred sources of error. Because of the relatively small sample sizes used in this study (8-20 individuals per population), it is likely that the range of morphological variation determined for each is less than that actually present. However, the relative location and size of each of the sample clusters on the PCA plot do give an indication of relative degrees of morphological variability within and between populations. The samples are time-averaged in that they comprise solely dead collected (1982-83), or a mixture of live and dead collected (1945-51) individuals. An attempt was made to minimise any temporal bias by including only shells of relatively freshly dead snails (shells with periostracum and apertural colouring) in the analysis. The statistically significant difference between apertural heights of the 1950-51 and 1982 West Island samples are probably caused by non-random sampling resulting from the preferential collection of large shells in 1950-51 (see Powell 1951: 132). The fact that the three extant Great Island colonies contained only very low numbers of snails/empty shells in 1945-46 (Powell 1948) indicates that collections made from them at that time are probably reasonably representative of actual contemporary morphological variability. However, the markedly disjunct grouping of individuals in the 1945 *P. b. bollonsi* sample as determined by PCA (Fig. 16) suggests the possibility that the morphologically distinct individual within that sample (an unlabelled shell in AK 25995, see Appendix 1) may in fact have been collected from North East Island (cf. Figs 14, 17).

Considering the above shortcomings within the data set, morphometric analysis supports Powell's (1948) contentions that the three extant *P. bollonsi* populations on Great Island have differing shell morphologies, and that shells from the extant *P. b. bollonsi* population above South East Bay are morphologically comparable with the *P. bollonsi* Suter holotype. Furthermore, it is apparent that characteristic shell morphologies have persisted within each of the populations from 1945-46 to 1982-83, although there is some indication that the overall range of morphological variation may have increased slightly in the *P. b. bollonsi* and *P. b. arbutus* populations during that time.

The analysis indicates that the range of morphological variation within the extinct Hapuka Point population is not directly comparable with that in the *P. b. arbutus* population as claimed by Powell (1948), but rather overlaps with those of all three extant populations on Great Island. Given the small size of the Hapuka Point sample (9 individuals) and wide spacing of its data points on the PCA plot, it is likely that the actual morphological variation within the original population was even greater.

Powell (1948, 1951) considered that shells from the West Island and North East Island populations were morphologically most similar to those from the *P. b. bollonsi* population on Great Island, but that is not supported by the present analysis. The West Island samples show a range of morphologic variation that is most similar to that of *P. b. caperatus*, albeit with shells from the former population typically being slightly smaller and having lower spire ratios (cf. Powell 1951; Tables 2, 3). The overall range of morphological variation within samples from the North East Island population overlaps with that of samples from both the *P. b. bollonsi* and *P. b. arbutus* populations on Great Island, although as pointed out by Powell (1948), the North East Island samples are most similar to *P. b. bollonsi* in terms of average shell height and spire ratio.

Differences in shell morphologies between geographically isolated populations of a land snail species can result from direct environmental influences on snail growth and shell shape, and/or from genetic differentiation by adaptive or non-adaptive selection, or by random processes (e.g. Jones *et al.* 1977; Goodfriend 1986). The differences in shell morphology between *P. bollonsi* populations are considered to be largely genetically controlled rather than phenotypes of environmental origin for two reasons. First, each of the three extant populations on Great Island has apparently retained distinctive and separate morphological characteristics from 1945-46 to 1982. If local environmental conditions were important in determining differences in shell morphology between the three small and locally restricted 1945-46 populations, it is unlikely that those shell characteristics would have continued to dominate in descendant populations, given the significant environmental changes that occurred on Great Island following the removal of goats in 1946. Probably as a consequence of their very limited geographic ranges, each of the 1945-46 populations were subjected to relatively homogeneous environmental settings in terms of substrate and vegetation type, litter cover and slope aspect (see Powell 1948). However, post-1946 expansion of ranges and population sizes coupled with marked albeit patchy habitat changes in vegetation and litter cover, meant that each of the colonies subsequently came to occupy a much wider range of environmental settings. That leads to the second reason for assuming that the morphological variation is largely genetic, that although the *P. b. bollonsi* and *P. b. arbutus* populations on Great Island each presently occupy a diverse albeit physically comparable range of habitat types (vegetation cover, substrate types, slope aspect, climate), the observed morphological differences between the two populations exceed intrapopulation variation. If environmental factors have an important inductive effect on *P. bollonsi* shell shape, the ranges of morphological variation of those two populations should be more comparable than they are.

Although the morphological characteristics of the extant *P. bollonsi* populations are here considered to be predominantly genetic, it is possible that some of that differentiation originally occurred as a result of environmental selection. In a review of the nature and causes of variation in size and form of land snail shells, Goodfriend (1986) noted that with many species, individuals living in moist conditions tend to be larger and have greater relative aperture areas than individuals in drier habitats. There is no comparable relationship evident within existing *P. bollonsi* populations between shell form and the various habitat types in which the species occurs, as noted above. However, such a correlation may have existed on Great Island in 1945-46, with individuals from the two populations that were restricted to boulder scree under remnant broadleaf groves (i.e. *P. b. bollonsi* and *P. b. arbutus*) typically having larger relative aperture areas and broader spires

than the *P. b. caperatus* individuals which were restricted to a (presumably) drier habitat under ngaio shrubs (see Powell 1948).

Although the observed differences in shell morphologies between the various *P. bollonsi* populations are probably largely genetic, a recent electrophoretic study by Triggs and Sherley (in press) based on samples of 5 snails from each of the North East Island and three Great Island populations, found only minor genetic differentiation between populations. That study showed that in terms of the 28 allozyme loci identified, the *P. b. bollonsi*, *P. b. caperatus* and North East Island populations were virtually genetically identical, and that the *P. b. arbutus* population differed from the other 3 only in terms of gene frequency. A further conclusion was that *P. bollonsi* has a low level of genetic polymorphism and heterozygosity.

Studies of some other landsnail species have also failed to find a consistent correlation between molecular differentiation and observed heritable shell characters within different populations (e.g. in *Cepaea*: Jones *et al.* 1977). In such cases, the nature of any molecular differentiation between populations may need to be resolved at the DNA level.

Biogeography and Morphological Differentiation

The genus *Placostylus* is widely distributed on continental and volcanic islands of Mesozoic and Cenozoic age in the southwest Pacific Ocean (Solem 1959), which, given a presumed limited ability to disperse across ocean basins, suggests that it had an eastern Gondwana origin. At present there are two subgenera of *Placostylus* in northern New Zealand that differ in anatomy and shell morphology (Haas 1935; Solem 1959; Climo 1973). The subgenus *Maoristylus* includes two closely related species, *P. (M.) hongii* Lesson in eastern Northland, and *P. (M.) ambagiosus* Suter in the Cape Reinga-North Cape area (Powell 1979), and the monotypic *Basileostylus* incorporates the Three Kings Islands endemic *P. (B.) bollonsi*.

There is no direct information on the Mesozoic-Cenozoic biogeography and phylogeny of *Placostylus* in New Zealand, with the oldest known fossils of the genus being of late Holocene age (Millener 1981). However, given what is known about the palaeogeography of the northernmost New Zealand region, *Placostylus* ancestral to the present-day *P. bollonsi* populations probably colonised the Three Kings Islands area in early Miocene time, and were subsequently isolated on the insular land masses that have persisted in that area from mid Miocene time to the present. During that period of about 15 Ma before the arrival of Maori at Three Kings Islands, there was probably a complex history of genetic differentiation within and between *Placostylus* populations in the area resulting from environmental factors such as changes in climate, habitat types, and the distribution and size of islands. It is logical to assume that an ancestral *P. bollonsi* population(s) would have been widely distributed across a single large island that existed on Three Kings Bank during the ultimate glacial period (i.e. prior to 11-14 Ka) and that subpopulations of that ancestral population could subsequently have become isolated on the four larger islands that formed within the Three Kings group during the period of post-glacial sea level rise. There were possibly inherited genetic differences between some or all of these isolated populations resulting from localised and/or clinal genetic differentiation within the ancestral population(s), and differentiation probably occurred within each island population as a consequence of major environmental changes (in climate and habitat types) caused by the transition from glacial to interglacial conditions.

Given the evidence for widespread anthropogenic habitat modification at Three Kings Islands during several centuries before 1840, it is not definitely known if the 5 surviving and 1 extinct populations of *P. bollonsi* all originated in situ, or whether the present-day locations of one or more resulted from translocations by Maori. Previous studies based on shell shape suggested that the North East Island population originated in prehistoric transfers of *P. b. bollonsi* snails from Great Island (Powell 1948, Climo 1973), and Powell (1951) proposed a similar origin for the West Island population. The morphometric analysis presented above shows clearly that shell shapes in the West Island population differ from those in any of the other *P. bollonsi* populations. Given the conclusion that shell shape within *P. bollonsi* is predominantly genetic, the simplest hypothesis is that the West Island 'race' differentiated in situ. It is impossible to determine from the morphometric data whether the North East Island population originated in situ, or resulted from transfers by Maori. The latter is a possibility given that the ranges of shell shape within the two populations are overlapping (not identical as previously claimed), but the simplest hypothesis on the basis of shell shapes alone is that the North East Island population, and those on Great Island, originated in situ.

During the period of Maori occupation of Three Kings Islands, widespread forest clearance probably isolated small remnant populations of *P. bollonsi* in steep, rocky areas on Great and North East Islands (Powell 1948), and possibly accounts for the absence of *P. bollonsi* on South West Island. In the early part of the 19th century until about 1840, *P. bollonsi* populations on Great Island were probably also adversely affected by domestic goats and pigs, and a subsequent reintroduction of goats to that island in 1889 led to severe habitat modification and consequent extinction or reduction in sizes of remnant *P. bollonsi* populations (Baylis 1948, Powell 1948, Turbott 1948). After eradication of goats in 1946 broadleaf trees and shrubs on Great Island regenerated widely and the three remaining *P. bollonsi* populations increased substantially in size and range. Similar increases in snail numbers probably also occurred on Great Island between 1840 and the 1890s in the absence of human inhabitants and before the build-up of goat numbers, and the snail population on North East Island had probably expanded to cover much of the formerly cultivated top of that island by the late 19th or early 20th century (Buddle 1948, Baylis 1958).

Possibly much of the observed morphological differentiation between *P. bollonsi* populations on Great Island is owing to "founder effects" resulting from population bottlenecks during the periods of Maori occupation and goat infestation. The fact that the now extinct Hapuka Point population had a range of morphological variation that substantially overlaps with those of the three extant populations on Great Island, lends support to this hypothesis. However, at least some of the differentiation between Great Island populations may have been inherited from a pre-Maori population(s), and/or have occurred in response to environmental factors during the last few hundred years. The range and size of the North East Island population were probably also significantly lower during the period of Maori occupation than at present, suggesting the possibility that it too could have been subjected to random selection processes resulting from population bottlenecks. West Island is apparently the only large island in the Three Kings group on which broadleaf forest and shrub communities escaped extensive modification (Baylis 1958), and it is unlikely that size, range or genetic diversity of that *P. bollonsi* "race" were ever significantly affected by anthropogenic activities.

Conservation Status

Historic records show that before the removal of goats from Great Island in 1946 the three *P. bollonsi* populations on that island were in danger of becoming extinct following progressive degradation of habitat caused by the browsing and trampling of goats (Powell 1948). Subsequent recovery of those snail populations is directly attributable to habitat improvement resulting from regeneration of broadleaf vegetation in the absence of goats. It is thus obvious that one of the most serious potential threats to the continued survival of *P. bollonsi* populations at Three Kings Islands would be renewed destruction or adverse disturbance of areas of broadleaf vegetation by fire, or from the introduction of browsing mammals or fungal pathogens (see comment by P.J. Brook in Wright & Cameron 1990). The other main potential threat is the introduction of mammalian predators such as rats or pigs, given the marked adverse effect those animals have had on *Placostylus* populations elsewhere (see Powell 1938, 1979; Iredale 1944; Penniket 1981). In the continued absence of such habitat modification the West Island and North East Island *P. bollonsi* populations will probably persist with similar numbers of snails as are present now, whereas the three populations on Great Island should continue to expand in size and range, and will presumably eventually amalgamate assuming broadleaf regeneration on that island continues. None of the *P. bollonsi* populations require any management intervention at present, but it would clearly be advantageous to acquire more detailed information on growth rates, population turnover, and ecological requirements of the species, should such intervention become necessary in the future.

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APPENDIX 1. Locality information for *Placostylus bollonsi* shells used for biometric and morphological analysis. AK = Auckland Museum collections, M = National Museum collections. (n) = number of specimens used for analysis. L01/ = grid references from NZMS 260 series maps (Department of Survey and Land Information).

Placostylus bollonsi bollonsi, Great Island

Holotype, National Museum	(1)	South East Bay landing slope. April 1907.
AK 25061	(3)	No. 1 location, ¼ mile NE of provision depot (ie. = No. 2 location of Powell 1948:283), November-December 1945.
AK 26288	(1)	500' in valley of SE landing (no date given, presumably 1945-1951).
AK 25995	(3)	No. 1 location, ¼ mile NW (ie. should be NE) of provision depot (see above), November- December 1945.
AK 76365	(1)	No. 1 location, NE of provision depot (see above), November-December 1945.
AK 75135	(20)	North side of South East Bay at c. 100 m elevation. L01/322832. December 1982.

Placostylus bollonsi caperatus, Great Island

AK71095, Holotype	(1)	Approximately 375' elevation, NW landing slope, April 1946.
AK 76366	(10)	As above.
AK 75137	(20)	Cliffs above North West Bay at c. 130 m elevation. L01/319830. December 1982.

Placostylus bollonsi arbutus, Great Island

AK 71094, Holotype	(1)	No. 2 location, SW coast (ie. = No. 5 location of Powell 1948:284); no date given, presumably November-December 1945.
AK 76367	(9)	As above.
AK 75133	(10)	W of trig station at c. 240 m elevation. L01/308827. December 1982.
AK 75134	(10)	Ridge NW of trig station at c. 260 m elevation. L01/30808275. December 1982.

Placostylus bollonsi sensu lato, Great Island (extinct)

AK 25062	(9)	Hapuka Point, Great Island (see Powell 1948:284), April 1946.
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Placostylus bollonsi sensu lato, West Island

AK 25064	(3)	West Island, 1951.
AK 25065	(3)	West Island, 1951.
AK 25066	(3)	West Island, December-January 1950.

- AK 26482 (3) West Island (no date given, presumably 1950 or 1951).
AK 75136 (20) Terrace at c. 100 m elevation at SE end of island. L01/222793. December 1982.

Placostylus boltoni sensu lato, North East Island

- AK 76364 (5) North East Island (no date given, presumably 1947 or 1948).
M 5853 (1) North East Island, ex Auckland Museum (no date given, presumably 1947 or 1948).
M 5859 (3) North East Island, January 1948.
AK 75132 (20) Top of island at c. 90 m elevation. L01/34258535. November 1983.
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